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Cytogenetics of mole rats of the *Spalax ehrenbergi* superspecies from Jordan (Spalacidae, Rodentia)

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Abstract

Karyotypes (chromosome sets and the banding patterns (G-, C- and Ag-NOR) of the *Spalax ehrenbergi* superspecies across 12 localities from Jordan are described for the first time. All mole rats from this region (excluding two individuals from Madaba with 2n = 62) have a diploid chromosome number of 2n = 60 but they display geographical variability in the number of autosomal arms (NFa = 68, 70, 72 and 74). The most widely distributed cytotype (from Madaba in the north to Wadi Musa, near Petra, in the south) has four pairs of small biarmed chromosomes. Karyotypes of two northern populations (Irbid and Zarqa) contain six pairs of small biarmed chromosomes. The intermediate karyotype with five small biarmed chromosomes is found 25 km north of Madaba, and a polymorphic population (Mt. Nebo) with five (2 animals) and four (4 animals) pairs of small biarmed chromosomes occurs between the northern and southern cytotypes. Geographical variability is also displayed by the short arm length in the first subtelocentric autosomes. All karyotypes have a similar C-banding pattern, with the exception of heterochromatin distribution in the variable first pair. Comparative analysis of G-banded chromosomes indicated that NF differentiation is due to pericentric inversions or centromere shift. Relationships between Jordanian, Israeli, and Turkish species of the *Spalax ehrenbergi* superspecies are discussed.

Key words: *Spalax ehrenbergi*, Jordan, chromosomal, differentiation

Introduction

The *Spalax ehrenbergi* superspecies occurs in the Near East from southern Turkey to Syria, Lebanon, Iraq, Israel, and Egypt with disjunction of the range in Sinai and the Nile delta. Comparative cytogenetical studies have shown that *S. ehrenbergi* consists of different allopatric chromosome forms with narrow hybrid zones in the territory of Israel (Wahrman et al. 1969 a, b; Wahrman et al. 1985). Interdisciplinary studies including cytogenetical, genetical, morphological, physiological, and behavioral peculiarities suggest that chromosome forms in this group represent good biological species, each adapted genotypically and phenotypically to a different climatic regime (Nevo 1991; Nevo et al. 1994 a, b; 1995). Seven chromosomal species of the *S. ehrenbergi* superspecies (3 from Turkey and 4 from Israel) with a different level of chromosomal differentiation are currently described (Wahrman et al. 1969 a, b; 1985; Yüksel 1984; Yüksel and Gülkaç 1992; Nevo et al. 1995). Comparative analysis of differentially stained chromosomes has made it possible to reveal the types of chromosomal rearrangements and has shown a more complicated composition of Turkish cytotypes and a relatively large cytogenetical distance between the Turkish and Israeli populations (Ivanitskaya et al. 1997). To inter-

pret the entire route of chromosomal evolution in this group, information on karyotypes from additional localities of the range (Syria, Iraq, Lebanon, and Jordan) is needed. Mole rats from Jordan are the most interesting because these populations are geographically the nearest neighbors to the Israeli populations. However, Israeli and Jordanian mole rats are separated by the Jordan and Arava rift valleys, and we might expect new chromosome forms in Jordan.

The purpose of this study was to describe mole rat karyotypes from Jordan to fill at least partially the gap in our knowledge about relationships between Turkish and Israeli *Spalax* species.

Material and methods

Mole rats (n = 69) were collected from 12 populations across their entire range in the Jordanian Mountain ridge in January and March 1996. The sampled localities and the number of individuals analysed are presented in table 1 and figure 1.

Chromosome preparations were obtained from bone marrow by a standard in-vitro method, following the yeast-stressing technique (Lee and Elder 1980). Differentially stained chromosomes were prepared by the trypsin method for G-bands (Seabright 1971) and by the BSG method for C-bands (Sumner 1972). Nucleolar organizer regions (NORs) were identified by the $AgNO_3$ colloidal-developer method of Howell and Black (1980).

Results and discussion

Karyotypes of all mole rats examined from Jordan (except two individuals from Madaba with 2n = 62) consisted of 60 chromosomes but differed in the number of autosomal arms (Tab. 1). The morphology of the sex chromosomes was stable: the X-chromosome was submetacentric and the Y-chromosome was acrocentric.

Chromosome sets of mole rats from the northern populations of Irbid and Zarqa (populations 1 and 2, Fig. 1) consisted of 8 pairs of biarmed and 21 pairs of acrocentric autosomes (NFa = 74). The short arms of the first subtelocentric pair were relatively long, usually longer than the short arms of the X-chromosome, but were variable in length (Fig. 2 a).

Table 1. Localities, sample size, diploid (2n) and fundamental (NFa) numbers for *Spalax* populations from Jordan

No. pop. in Fig. 1	Locality	N males	N females	2n	NFa
1	Irbid	5	3	60	74
2	Zarqa	3	7	60	74
3	25 km north of Madaba	3	2	60	72
4	Mt. Nebo	2	4	60	72, 70
5	Madaba	4	5	60, 62	68, 70
6	10 km east of Madaba	2	2	60	68
7	Dhiban	2	4	60	68
8	South of Wadi Mawjib	–	5	60	(70)
9	Karak	1	3	60	(70)
10	South of Mazar	1	2	60	(70)
11	8 km north of Tafila	1	2	60	70
12	Upper Wadi Musa	4	1	60	70

NFa in some populations are in parentheses because of variable morphology of the first pair of chromosomes

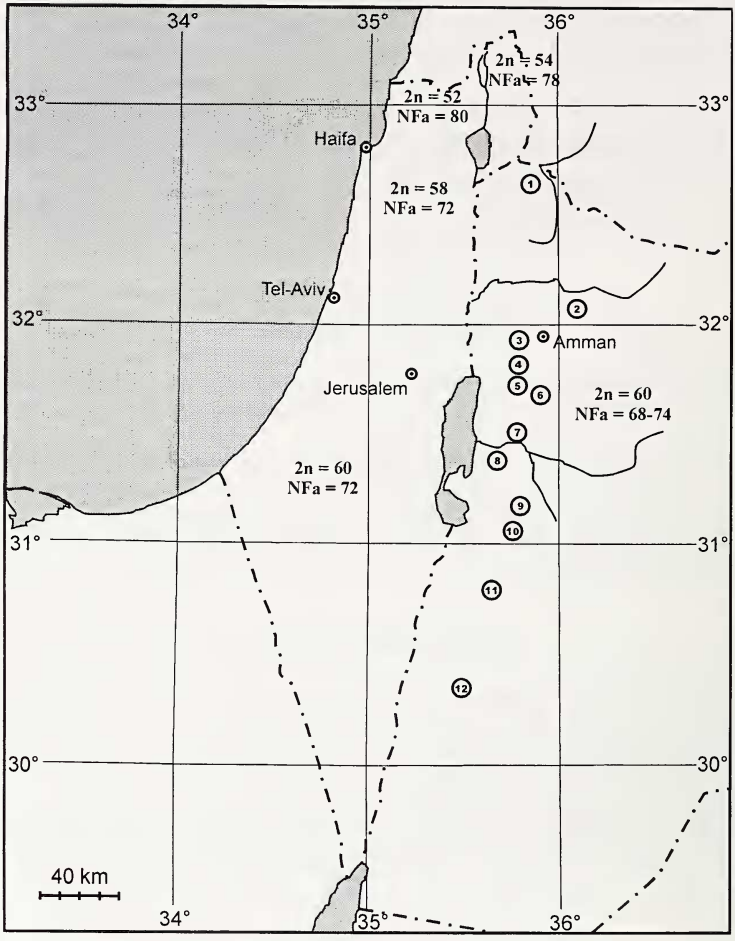

Fig. 1. Collecting localities of mole rats in Jordan and distribution of chromosome species in Israel. 1. Irbid, 2. Zarqa, 3. 25 km north of Madaba, 4. Mt. Nebo, 5. Madaba, 6. 10 km east of Madaba, 7. Dhiban, 8. south of Wadi Mawjib, 9. Karak, 10. south of Mazar, 11. 8 km north of Tafila, 12. upper Wadi Musa.

All individuals examined from population 3 (25 km north of Madaba) had 7 pairs of biarmed chromosomes and 22 pairs of acrocentrics in the autosomal complements (NFa = 72). The short arms in the first pair of autosomes were smaller than the short arms of the X-chromosome, displaying slight length variability (Fig. 2 b).

The population from Mt. Nebo was polymorphic on the number of autosomal arms caused by a different number of small biarmed chromosomes: two individuals had five pairs chromosomes in this group, and four individuals had four pairs of small biarmed autosomes (NFa = 74, 70). The first pair of chromosomes was subtelocentric but with very small short arms that were smaller than in the north of Madaba population (Fig. 2 d, e).

Almost all mole rats from populations 5, 6, and 7 (Madaba regions and Dhiban) had identical karyotypes. The variable group of small biarmed autosomes consisted of four pairs and the first pair was always acrocentrics (NFa = 68). One male and one female from Madaba had an unusual karyotype for *S. ehrenbergi*, consisting of 2n = 62, i. e. with one pair of small extra-number acrocentric chromosomes (Fig. 2 d).

All mole rats from populations 8–12 had four pairs of small biarmed autosomes but displayed geographical variability in the morphology of the first autosomal pair (Fig. 2 f, g, h). These chromosomes were subtelocentrics with short arms that were similar in length to short arms in the X-chromosome in southern populations (Tafila and Wadi Musa). The first subtelocentrics had very small short arms, sometimes invisible in conventional stained spreads, in the Mawjib, Karak, and Mazar populations. Intrapopulation and also intraindividual variability of these arm lengths were more remarkable in populations 8, 9, 10.

Fig. 2 a–c

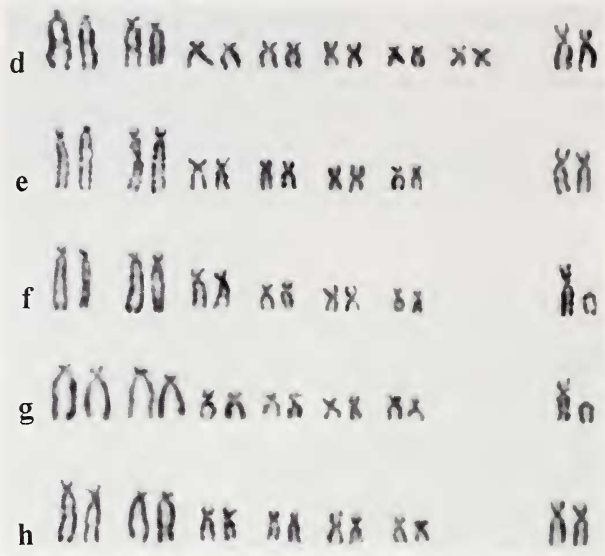

Fig. 2. Conventional stained karyotypes of some *S. ehrenbergi* cytotypes from Jordan: a female from Irbid (2n = 60, NFa = 74); b male from locality N 3 (25 km north of Madaba) (2n = 60, NFa = 72); c female from Madaba (2n = 60, NFa = 68), the small acrocentric pair in the frame is the extra-numeral chromosomes from a male karyotype with 2n = 62; d, e, f, g, h fragments of karyotypes containing biarmed autosomes and sex chromosomes of cytotypes: d female from Mt. Nebo with NFa = 72; e female from Mt. Nebo with NFa = 70; f male from Mazar; g male from Tafila; h female from Wadi Musa (2n = 60, NFa = 70).

C-banding patterns

All Jordanian mole rat cytotypes had a similar distribution and amount of heterochromatin material (Fig. 3). Acrocentric chromosomes bore more or less large blocks of pericentromeric heterochromatin; biarmed autosomes, excluding the first pair, were usually C-negative, and dot-like pericentromeric or telomeric blocks that were revealed in some of these chromosomes were unstable within population. The very small C-blocks in centromeric regions of the X-chromosomes were not as dark as in the autosomes; the Y-chromosomes were C-negative (Fig. 3 b, e). „Additional" chromosomes in karyotypes of two individuals from Madaba did not differ in their C-banding from the other acrocentric autosomes and seem to be the smallest ones (Fig. 3 c).

The greatest interpopulation differentiation in C-banding patterns was revealed in the first pairs of autosomes. These chromosomes in cytotypes from Irbid and Zarqa bore C-blocks localized in pericentromeric and undercentromeric regions of the long arms; the short arms were C-negative (Fig. 3 a). Cytotypes from populations 3 and 4 with a variable first pair possessed pericentromeric heterochromatin and more or less intensively C-stained short arms (Fig. 3 b). The first pair in cytotype from Dhiban and Madaba was acrocentric with pericentromeric C-block and was distinguishable from the other acrocentric autosomes only by its size and the presence of two bands in the middle of the arms (Fig. 3 c). Populations from Mawjib, Karak, and Mazar were highly variable for short arm length variability in the first pair displaying both intra- and interpopulation variability in C-banding patterns of this pair. Pericentromeric heterochromatin blocks may have been absent (Fig. 3 d) or similar to C-blocks of acrocentric pairs (Fig. 3 e). The short arms and the regions close to the centromeres of the long arms were stained more

intensively than euchromatin material, differing in size and intensity (Fig. 3 d, e). The first pairs in karyotypes from the southern populations (Tafila and Wadi Musa) which were more or less stable in the morphology displayed C-banding patterns very similar to the Mawjib cytotype (Fig. 3 d).

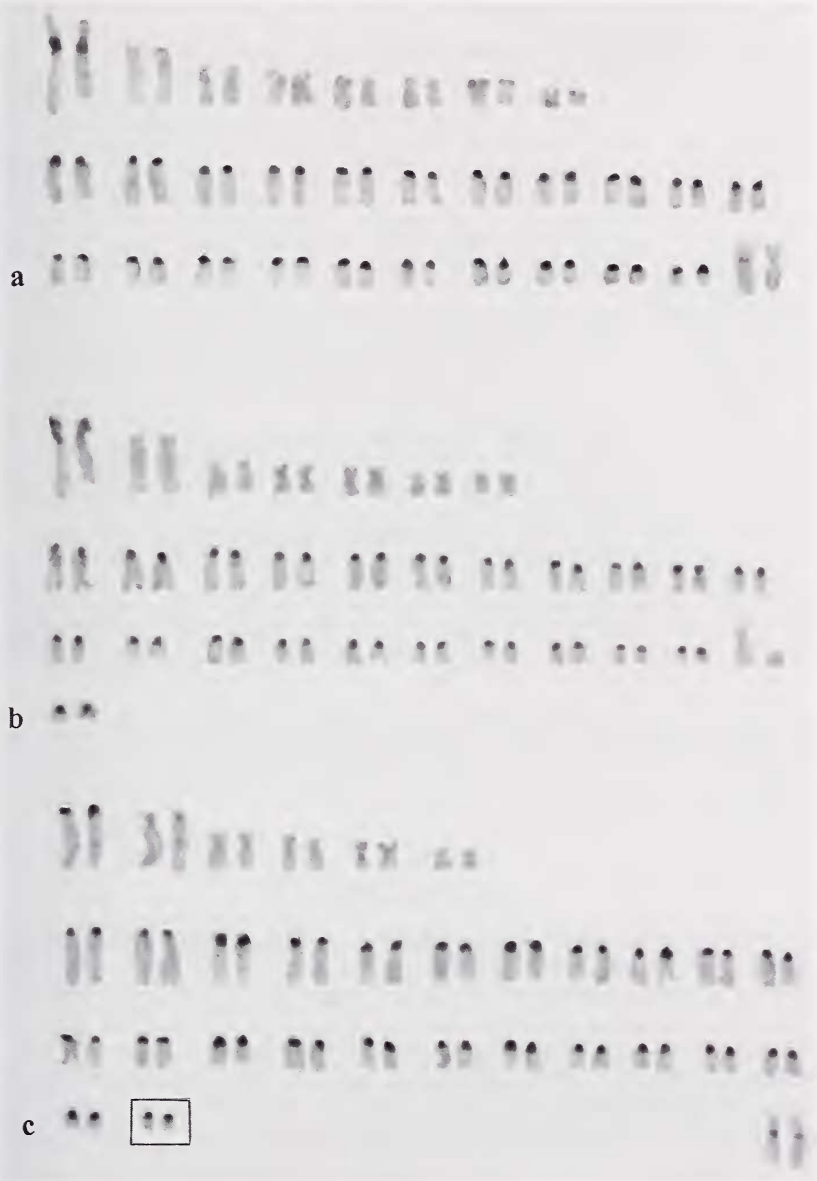

Abb. 3 a–c

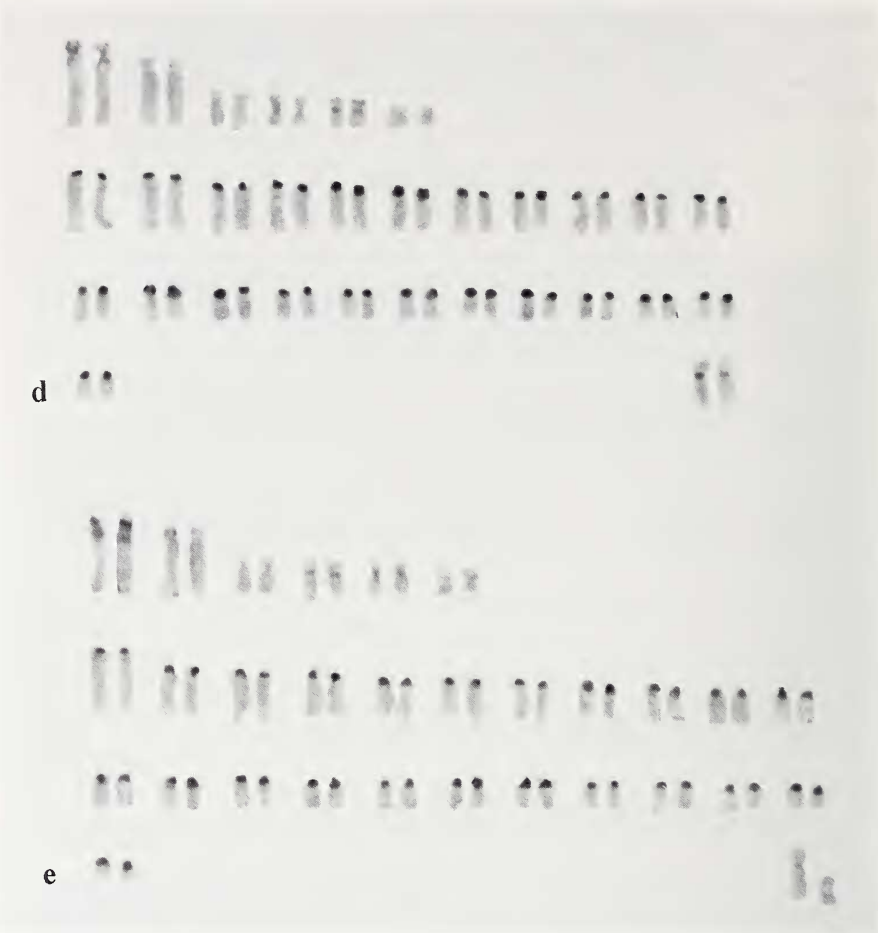

Fig. 3. Distribution of heterochromatin in different cytotypes of *S. ehrenbergi* from Jordan: a C-banding pattern in a female from Irbid (NFa = 74); b male from 25 km north of Madaba (NFa = 72), c female from Madaba (NFa = 68), the acrocentric pair in the frame is the extra-numeral chromosomes from the male karyotype with 2n = 62; d female from Wadi Mawjib (NFa = 70); e male from Karak with very small short arms in the first chromosome (NFa = 70).

G-banding patterns

G-stained chromosomes of four populations of *S. ehrenbergi* from Irbid (I) (NFa = 74), 25 km north of Madaba (N) (NFa = 72), Madaba (M) (NFa = 68), and Tafila (T) (NFa = 70) are presented in figure 4. Obviously, almost all of the chromosomes of these karyotypes displayed similar patterns of G-band sequences. The essential difference between populations concerned the group of small biarmed chromosomes. Four pairs from this group (3, 4, 5, 6) had identical morphology with the same G-banding patterns in all populations. The smallest pair (29) in karyotypes with NFa = 74 was metacentric instead of acrocentric in other karyotypes; the acrocentric condition of pair 26 in karyotypes with NFa = 74, 70, and 68 was replaced by metacentric in karyotype with NFa = 72 (group C in Fig. 4). Because of the small size of these chromosomes and the limited number of G-bands it cannot be stated with certainty what type of rearrangement (pericentric inver-

sion or centromere shift) is responsible for the change in centromeric position. Mole rats from Irbid and Zarqa (NFa = 74) differed from other populations by the biarmed condition of pair 7, which according to Wahrman et al. (1985) belongs to the unchangeable group A of Israeli *S. ehrenbergi*. Considering the same sequence of G-bands in acrocentric and biarmed chromosomes of pair 7, the centromere shift is a more likely type of the rearrangement.

The acrocentric condition of the first autosomal pair in the cytotype with NFa = 68 may be explained by pericentric inversion of the formerly subtelocentric chromosome with very small short arms. This is confirmed by the replacement of the dark G-band, lo-

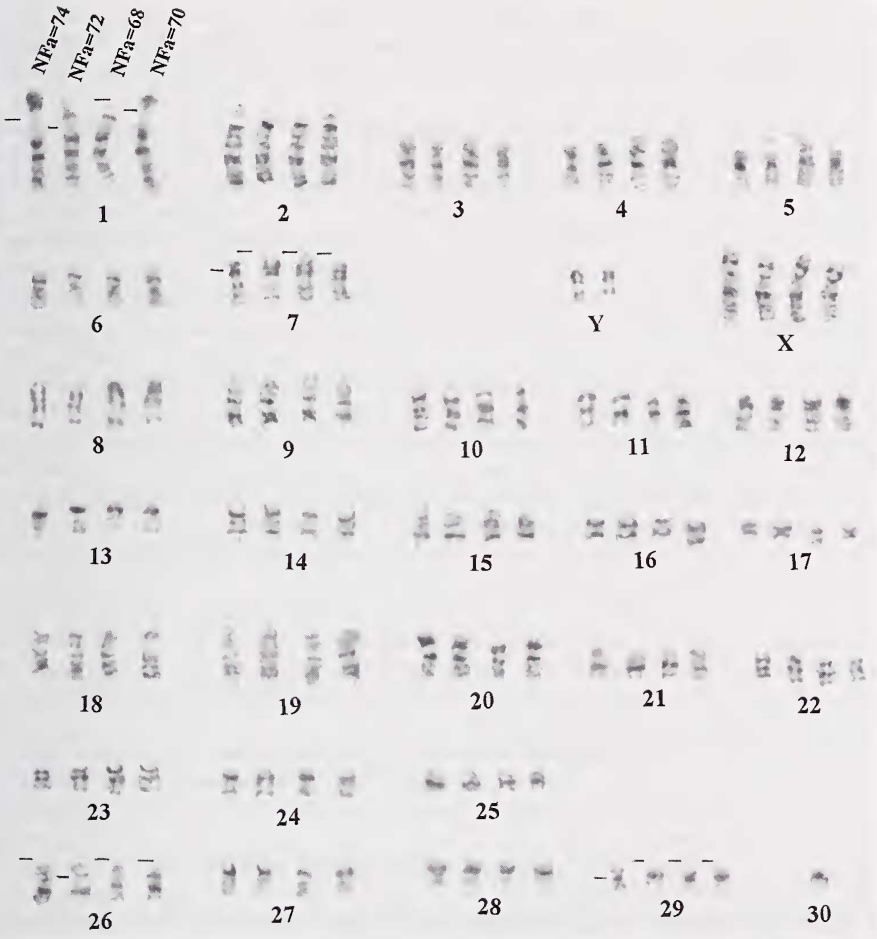

Fig. 4. G-banding patterns of haploid sets of four cytotypes from Jordan. From left to right: Irbid (NFa = 74), 25 km north of Madaba (NFa = 72), Madaba (NFa = 68), Tafila (NFa = 70). Chromosomes are arranged according to Wahrman et al. (1985) classification: autosome 1–17 belong to the group A (unchangeable chromosomes in Israeli *Spalax*), autosomes 18–25 belong to the group B with Robertsonian type of rearrangement in Israeli *Spalax*, autosomes 26–29 belong to the group C with variable centromere position. Chromosome N 30 is "additional" acrocentric in a male karyotype from Madaba (2n = 62). Chromosomes 8–25 are acrocentrics; dashes indicate the centromere positions in groups A and C.

cated above centromeres in subtelocentric chromosomes, under the centromeric region in acrocentric ones. Variability of the short arm lengths in the first pair autosomes was reflected in their G-banding patterns. Relatively long arms in the cytotype from Irbid and Zarqa had numerous dark bands located close to each other, so that the short arms in these karyotypes usually resembled dark uniformly stained material. Karyotypes with small short arms of the first subtelocentric pair usually had one dark G-band adjacent to the centromeric region (Fig. 4).

Nucleolar organizing regions

Two types of N-banding patterns among Jordanian mole rats were revealed. Cytotypes with NFa = 74, 72, and 70 possessed two NORs-bearing chromosome pairs, and the cytotype from Madaba and Dhiban (NFa = 68) had one pair with NORs. These chromosomes (the first subtelocentrics and fifth metacentrics in Fig. 4) can be recognized on conventional, C-, and G-stained spreads also.

We now have more or less complete information on mole rat karyotypes from Jordan. Despite the distribution of Jordanian mole rats more than 100 km south of the Israeli *Spalax*, no variability in chromosome numbers was found in Jordan. The presence of two individuals in Madaba with 2n = 62 is unexplainable by centromeric fission, because 17 individuals with an acrocentric condition of the first pair had 2n = 60. In addition, the acrocentric morphology of the first pair in the karyotype with NFa = 68 originates from pericentric inversion (and not fission), as follows from comparative analysis of G-banded chromosomes. It is difficult to explain the reason for the appearance of the smallest "additional" acrocentric chromosomes in the *S. ehrenbergi*, karyotype. We emphasize only that this type of chromosomal polymorphism in *S. ehrenbergi* is the first on record.

The main difference among Jordanian cytotypes is caused by pericentric inversion or centeromeric shifts in four chromosomal pairs. Two of these pairs belonging to the group C. Pericentric inversions in chromosomes from this group are responsible for the NF variation among Israeli cytotypes of mole rats (Wahrman et al. 1985). Change of centromere position in the first and seventh pairs of chromosomes from group A in some Jordanian *Spalax* (Fig. 4) is the principal rearrangement that differentiate Israeli (2n = 60) and Jordanian mole rat cytotypes. Conventional stained karyotypes of the Israeli cytotype with 2n = 60, NFa = 72 and Jordanian cytotype from the northern Madaba population (Fig. 2 b) are seemingly identical, but G-banding method made it possible to show differentiation between them caused by an altered position of centromeres in two chromosome pairs. Furthermore, Israeli cytotypes with 2n of 52, 54, and 58 differ from Jordanian cytotypes by series of Robertsonian rearrangements.

The karyotypes of two geographically close populations form Afiq (2n = 58, NFa = 72) and Irbid (2n = 60, NFa = 74), 20 km apart, differ by one Robertsonian translocation and one pericentric inversion. The presence of biarmed condition in the 7th pair of autosomes in the Irbid and Zarqa cytotype links it with Israeli cytotypes and differentiates them from the other Jordanian cytotypes with the acrocentric morphology of this pair. The northern distribution of the Irbid cytotype is restricted by the Yurmuk river and in any case the southern Golan Afiq population with 2n = 58 is apparently a recent colonizer from the Lower Galilee mountains. The southern border of the Irbid cytotype is possibly Wadi Sir. Wadi Sir and Mt. Nebo mole rats prevail with NFa = 72. The population from Mt. Nebo is polymorphic: two of the animals had karyotypes with NFa = 72, like the northern cytotype, and four individuals had NFa = 70, karyologically identical with the southern cytotype (Mawjib, Karak, Mazar), differing from the nearby Madaba cytotype. The small sample from Mt. Nebo does not permit an explanation of the origin of chromosomal variability in this population. We cannot exclude a hybrid origin of this population, but the existence of the intergradation zone in this region is more likely.

Comparative analysis of C-banded chromosomes revealed low interpopulation variability of heterochromatin contents, except for C-banding patterns of the first subtelocentric autosome. These chromosomes in all cytotypes bear heterochromatin material, but the type of localization and its abundance yield specific patterns for different cytotypes (Fig. 3). Intrapopulation heterochromatin variability in these chromosomes is absent in the cytotype with NFa = 68, and more or less developed in cytotypes with subtelocentric morphology of these chromosomes. The higher the intrapopulation variability of the short arm length, the more changeable are the C-banding patterns. The first subtelocentric chromosomes in the Israeli *Spalax* are characterized by high variability in the length of both arms. Nevertheless, these chromosomes in all examined populations from Israel were C-negative (Wahrman et al. 1985).

In contrast to Israeli, Jordanian, and also Egyptian (Lay and Nadler 1972) species, Turkish mole rats do not possess size variability in the first pair (Ivanitskaya et al. 1997). These chromosomes in Turkish populations are either subtelocentric without remarkable variability in arm length, or acrocentric. The short arms of this chromosome in the *S. leucodon* superspecies are completely heterochromatic, and they have telomere C-bands in some 2n = 52 populations of *S. ehrenbergi*. The acrocentric condition of this pair in two Turkish cytotypes is caused by centromeric fission and not by pericentric inversion as in Jordanian cytotype from the Madaba and Dhiban region. Thus, this chromosome pair was presumably subjected to different types of rearrangements and should be excluded from the group of unchangeable chromosomes (group A in Wahrman et al. 1969, 1985). Also, chromosome pair N 7 (Fig. 4), which has an invariable biarmed morphology in the Israeli cytotypes, is replaced by acrocentric chromosomes in all Turkish species and in most Jordanian cytotypes. After combining all data on *S. ehrenbergi* karyotypes, group A will consist of 10 autosomal pairs, instead of 17 in Israeli species.

Summarizing the data on G- and C-banded chromosomes in mole rats makes it possible to conclude that the level of chromosomal divergence among Jordanian cytotypes is lower than among Turkish cytotypes, and even among Israeli mole rats. The discovery of new chromosomes involved in rearrangements in the Jordanian *Spalax* in comparison with Israeli species supports the hypothesis that more or less independent chromosomal evolution took place in these adjacent regions.

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Zusammenfassung

Zytogenetik von Blindmullen der Spalax ehrenbergi-Superspezies aus dem Jordanland (Spalacidae, Rodentia)

Karyotypen (Chromosomensätze und Muster von G-, C- und Ag-NOR-Bänderungen) der *Spalax ehrenbergi*-Superspezies aus 12 Gebieten des Jordanlandes werden neu beschrieben. Alle Blindmulle aus dieser Region (mit Ausnahme von zwei Individuen aus Madaba mit 2n = 62) hatten eine diploide Chromosomenzahl von 2n = 60, aber sie zeigten geographische Variabilität hinsichtlich der Zahl der autosomalen Arme (NFa = 68, 70, 72 und 74). Der am weitesten verbreitete Zytotyp (von Madaba im Norden bis zum Wadi Musa, nahe Petra, im Süden) hatte vier Paar kleine zweiarmige Chromosomen. Karyotypen der beiden nördlichen Populationen (Irbid und Zarqua) besaßen sechs Paar kleiner zweiarmiger

Chromosomen. Der intermediäre Karyotyp mit fünf kleinen zweiarmigen Chromosomen fand sich 25 km nördlich von Madaba; eine polymorphe Population (Mt. Nebo) mit fünf (2 Tiere) und vier (4 Tiere) Paar kleiner zweiarmiger Chromosomen kam zwischen den nördlichen und südlichen Zytotypen vor. Geographische Variabilität zeigte sich auch hinsichtlich eines sehr kurzen Armes beim ersten Paar subtelozentrischer Autosomen. Mit Ausnahme der Heterochromatinverteilung im ersten variablen Chromosomenpaar hatten alle Karyotypen ähnliche C-Bandenmuster. Eine vergleichende Analyse der Chromosomen mit G-Bänderung ergab, daß die NF-Differenzierung auf perizentrische Inversionen oder Zentromerverschiebungen zurückgeht. Die Beziehungen zwischen jordanischen, israelischen und türkischen Arten der *Spalax ehrenbergi*-Superspezies werden diskutiert.

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